PAN-PACIFIC ENTOMOLOGIST
69(2): 117–121, (1993)

GROUP FORAGING FACILITATES FOOD FINDING IN A SEMI-AQUATIC HEMIPTERAN, *MICROVELIA AUSTRINA* BUENO (HEMIPTERA: VELIIDAE)

Steven E. Travers[1]
Department of Biological Sciences, University of Kentucky,
Lexington, Kentucky 40506

Abstract.—Group living may evolve as a result of individuals finding food more quickly when in the presence of others versus when alone. Food location by individuals may facilitate food location by others in the group, and may increase mean search rate (food patches found/time) relative to solitary foraging. I experimentally addressed the influence of group foraging on the mean and variance in food-finding time (inverse of search rate) of a semiaquatic bug, *Microvelia austrina* Bueno. Focal males and females were observed in the lab in two contexts: alone versus in the presence of seven conspecifics. Food-finding time and movement rate were calculated for 29 focal animals in each context. Both the mean and variance in food-finding time decreased significantly when focal animals foraged in groups versus alone. Faster microveliids had shorter food-finding times. However, the decrease in food-finding times in groups is most likely due to foraging animals being attracted to conspecifics that have located food, rather than movement rate differences between foraging contexts. This is the first study to show search rate benefits to group living in an insect.

Key Words.—Insecta, Hemiptera, Veliidae, group living, facilitation, foraging behavior

Group living can affect individual feeding rates (Pulliam & Caraco 1984). The influence of group living on the mean and variance in the rate at which food, or food patches, are found has received much experimental attention. If group living has evolved in some species as a result of foraging advantages, then individuals are expected to locate food less frequently when foraging alone versus in a group. Individuals in groups often have higher mean and/or lower variance in search rate (food patches found per unit time) than solitary individuals. These patterns have been demonstrated experimentally in birds (Krebs et al. 1972, Brown 1988) and fish (Pitcher et al. 1982). However, very few experimental studies have examined the effects of group living on search rate in invertebrates (but see Rypstra 1989, Uetz 1988).

The semi-aquatic insect *Microvelia austrina* Bueno (Veliidae) is commonly found clustered in groups of up to 100 individuals (Travers & Sih 1991) on the surface of stream pools. They are opportunistic feeders on floating soft-bodied organisms, such as anopheline larvae and muscid flies (Anderson 1982), and will collectively feed on large items (personal observation). I conducted an experiment on field-caught microveliids to test the predictions that: (1) foraging in groups, versus alone, decreases both the mean and variance in time until a food item is found (hereafter food-finding time); and (2) the food-finding time of an individual is a function of the individual's movement rate (number of moves per unit time).

---

[1] Current address: Department of Biological Sciences, University of California, Santa Barbara, California 93106.

MATERIALS AND METHODS

Adult *M. austrina* were collected from a second order stream, 30 km south of Lexington, Kentucky, and maintained in the laboratory for four days prior to experimental trials. All animals were fed frozen fruit flies (*Drosophila melanogaster* Meigen) *ad libitum* up until 48 hours prior to the experiment. Twenty-four hours prior to the experiment, focal males and females were isolated and marked on the pronotum with a fine, red powder.

I measured the food-finding times of focal individual microveliids foraging in two separate contexts: alone and in the presence of seven conspecifics of the same sex. The sexes were tested separately to prevent mating, which would reduce the number of animals searching for food. Fifteen focal males and fourteen focal females were monitored in both treatments (solitary and group). Seven of the males and females were monitored in the solitary treatment first (SG). The other eight males and seven females were monitored in the group treatment first (GS). Individuals were randomly assigned to GS or SG sequences.

All experimental trials were conducted in a plastic tub (19 × 30 cm) filled to a depth of 4 cm with tap water. To prevent microveliids from detecting surface vibrations that are associated with the introduction of food, all experimental animals were placed on one side of an aluminum foil barrier while two frozen, adult fruit flies were placed 7 cm apart on the other side of the barrier. Trials began when I lifted the barrier. The following information was recorded with a hand-held tape recorder during a trial: (1) time of trial initiation, (2) time of food location by the focal individual, and (3) the number of movements by the focal individual (microveliids move in a saltatory fashion with discrete starts and stops). Trials were terminated after the focal animal found the first fly. I then calculated: (1) the time required for each focal individual to find food when in a group versus when alone, (2) the overall movement rate (number of moves per second) of focal individuals while foraging alone, and (3) movement rates before and after food discovery by a conspecific in group trials.

To compare food-finding times in solitary and group treatments, I used a one-tailed paired *t*-test because I had the *a priori* expectation that food-finding times for individuals in groups would be lower than that of the same individuals when alone. The variance in food-finding time was compared between treatments using a *F*-ratio test. To test for effects of gender or trial sequence (SG or GS), I conducted two-way analysis of variance (ANOVA) on food-finding times and movement rates of focal animals (when alone, in a group, before versus after food discovery by a conspecific). All values for ANOVAs were log-transformed to reduce heteroscedasticity.

Individuals varied considerably in food-finding time. To test the hypothesis that more active foragers find food sooner, I regressed food-finding time against movement rate in the same trial. I pooled the data for all analyses because in most cases there were no significant gender or sequence effects (although after food discovery females moved more frequently than males: $F = 8.96$, $P = 0.009$).

RESULTS

Group foraging significantly reduced the food-finding time of focal animals by, on average, 55.7% ($\bar{x} \pm$ SD: solitary trials = 243.8 ± 58.3 sec, group trials = 107.9 ± 14.7 sec; paired *t*-test: $t = 2.21$, $P = 0.02$). Movement rate was significantly, negatively related to food-finding time when animals foraged alone ($r^2 = 0.59$, df = 28, $P = 0.0007$) and in groups ($r^2 = 0.372$, df = 28, $P = 0.047$); i.e., less active animals took longer to find food. Focal animals also showed significantly lower variances in food-finding time when foraging in groups versus alone (*F*-ratio test: $F = 15.7$, $P = 0.0001$).

Foragers were significantly more active when foraging alone than when foraging in a group (mean moves/sec ± SD: solitary trials = 0.66 ± 0.1, group trials = 0.50 ± 0.02; paired *t*-test: $t = 3.02$, $P = 0.005$). Male movement rate did not differ significantly before versus after food discovery (paired *t*-test: $t = 0.13$, $P = 0.90$). Females showed a nearly significant tendency to move faster following food discovery ($t = 2.20$, $P = 0.06$).

DISCUSSION

This study is the first to address the effects of group foraging on foraging success in an insect. As has been the case for many vertebrates, the mean and variance in food-finding time were lower for foragers in groups. On average, *M. austrina* thus enjoyed group benefits in search rate.

The search rate of microveliids depends in part on the rate at which they are moving. Interestingly, despite a negative relationship between an individual's movement rate and food-finding time within both group and solitary treatments, focal animals (1) had lower movement rates when in groups than when alone and (2) found food sooner when in groups. This apparent contradiction is most likely due to an increased proportion of movements being directed towards food items for focal microveliids in groups relative to those foraging alone. Foraging microveliids quickly responded to conspecifics that located food by moving in the direction of the feeding animal(s). In 20 out of 29 (69%) group foraging trials, the focal animal arrived at the food item after a conspecific. This interaction, termed "local enhancement," whereby individuals intentionally or unintentionally communicate the location of food to others (Krebs et al. 1972, Pitcher et al. 1982), may rely on surface waves created by actively feeding microveliids. Thus, despite the fact that microveliids in group contexts move less frequently per time unit relative to when alone, a larger proportion of the moves are towards food because of cues provided by successful microveliids; this results in lower food-finding times. Within each one of these foraging contexts, faster animals locate food sooner.

A likely mechanism for the location of successful foragers is detection of vibrations through the surface tension of water. Wilcox (1979) found that rapid movement of tarsi by water striders (*Gerris remigis* Say) on the water surface effectively communicates gender of one male to another male. Successful microveliids increased the movement rate of their tarsi upon finding food. Furthermore, other foraging microveliids seemed to move in the direction of the successful microveliid after its discovery. An intriguing possibility in this scenario is that the communication of food whereabouts is intentional, suggesting altruism on the part of successful foragers. Given a few assumptions (see Trivers 1971), intentional communication between all members of a population should evolve if the decrease in food-finding time associated with group foraging translates into fitness benefits. An individual can only gain the benefit of decreased food-finding times by cooperating with conspecifics that signal. However, once that individual cooperates (signals), the cost of cooperation (sharing its find) will be outweighed by the benefit of shorter mean food-finding times in the long run, improving the individual's fitness.

Variance in food-finding time was lower in group foraging, as has been observed in other animals (Krebs et al. 1972, Brown 1988, Pitcher et al. 1982). Because my main goal in this experiment was simply to test for this relationship, I have no further data on whether microveliids switch to solitary foraging (risk-sensitive) when starved, as predicted by theory (Caraco 1980). Further experiments on this question may illuminate some of the selective forces responsible for the evolution of group living in this species.

The rate at which food items are encountered is only one of several components influencing a forager's rate of energy gain. Although an individual microveliid may find more food items per unit of time when in a group, the individual may gain less energy/time than a solitary forager because grouped microveliids are forced to share prey with conspecifics (see Clark & Mangel 1986). On the other hand, there may be a premium on finding food quickly because of behavioral tradeoffs between foraging, predation risk and mating behavior. Predatory sunfish (*Lepomus cyanellus* Rafinesque) and water striders (*Gerris remigis*) are known to disrupt the mating behavior (Travers & Sih 1991) and alter habitat use (Sih 1988) of *Microvelia austrina.* Thus, longer food-finding time for solitary individuals may lead to mating and predation costs that outweigh the benefits of feeding alone. Faster location of food resources may also be advantageous despite reduced per patch reward given the ephemeral nature of acceptable food floating downstream. Further experiments examining energy gains of individual microveliids foraging in groups and in field situations will be informative.

ACKNOWLEDGMENT

I thank Andy Sih, Phil Crowley, Craig Sargent, Roland Knapp, and Susan Mazer for their useful comments on this manuscript. Data collection in this study would have been impossible without the flawless assistance of Beth Karson.

LITERATURE CITED

Anderson, N. M. 1982. The semiaquatic bugs. Scandinavian Science Press Ltd., Klampenborg, Denmark.

Baker, C. M., C. S. Belcher, L. C. Deutsch, G. L. Sherman & D. B. Thompson. 1981. Foraging success in junco flocks and the effects of social hierarchy. Anim. Behav., 29: 137–142.

Brown, C. R. 1988. Enhanced foraging efficiency through information centers: a benefit of coloniality in cliff swallows. Ecology, 69: 602–613.

Caraco, T. 1980. On foraging time allocation in a stochastic environment. Ecology, 61: 119–128.

Clark, C. W. & M. Mangel. 1986. The evolutionary advantages of group foraging. Theor. Popul. Biol., 30: 45–75.

Krebs, J. R., M. H. MacRoberts & J. M. Cullen. 1972. Flocking and feeding in the great tit *Parus major*—an experimental study. Ibis, 114: 507–530.

Pitcher, T. J., A. E. Majurran & I. Winfield. 1982. Fish in larger shoals find food faster. Behav. Ecol. Sociobiol., 10: 149–151.

Pulliam, H. R. & T. Caraco. 1984. Living in groups: is there an optimal group size? pp. 122–147. *In* Krebs, J. R. & N. B. Davies (eds.) Behavioural ecology (2nd ed.). Blackwell, Oxford.

Rypstra, A. L. 1989. Foraging success of solitary and aggregated spiders: insights into flock formation. Anim. Behav., 37: 274–281.

Sih, A. 1988. The effects of predators on habitat use, activity and mating behaviour of a semi-aquatic bug. Anim. Behav., 36: 1846–1847.

Travers, S. E. & A. Sih. 1991. The influence of starvation and predators on the mating behaviour of a semi-aquatic insect, *Microvelia austrina.* Ecology, 72: 2123–2136.

Trivers, R. 1971. The evolution of reciprocal altruism. Q. Rev. Biol., 46: 35–57.

Uetz, G. W. 1988. Group foraging in colonial web-building spiders: evidence for risk-sensitivity. Behav. Ecol. Sociobiol., 22: 265–270.

Wilcox, R. S. 1979. Sex discrimination in *Gerris remigis*: role of a surface wave signal. Science, 206: 1325–1327.

Received 21 November 1991; accepted 25 November 1992.